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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR.—No. 151.

THE SENSE OF HEARING IN THE GOLDFISH CARASSIUS AURATUS L.

HENRY B. BIGELOW.

I. INTRODUCTION.

TO THE older investigators, such as Hunter (:82) Müller ('48), and Owen ('66), the presence of internal ears in fishes was sufficient evidence that these animals had a sense of hearing. Kreidl ('95), however, was the first to seek experimental evidence on this point. He tested normal goldfishes, and others from which he had removed the semicircular canals with the attached portions of the ears. Since both classes of fishes reacted similarly to sounds, he concluded that the skin, not the ear, is stimulated by sound, and that, therefore, it can be said that goldfishes do not hear. This conclusion has since gained considerable recognition, and has been accepted by Mulertt (:02) in his recent book *The Goldfish*. Kreidl ('96) also made observations on the trout in the fish basins of the Benedictine Monastery at Krems, Austria, and gathered ample evidence to prove that the belief that the fish assembled for food at the ringing of a bell to be unfounded. These observations confirmed him in the opinion that fishes do not hear, a conclusion further supported by the subsequent observations of Lee ('98) on other species, particularly the dogfish.

In spite of this important evidence, Lang (:03) concludes a popular discussion of the question "Do acquatic animals hear?" with the statement that fishes and other like forms should be tested more extensively before a decisive answer can be given. Tullberg (:03), whose experiments led him to conclude that the fish ear receives stimuli from currents in the surrounding water,

admits the possibility that the ear may also be in some degree an organ of hearing. The fact that certain fishes do respond to what are beyond question sound vibrations in water was demonstrated independently by Zenneck (:03) for three fresh-water species, *Leuciscus rutilus*, *L. dobula*, and *Alburnus lucidus*, and by Parker (:03[a], :03[b]) for a salt-water species, *Fundulus heteroclitus*. Parker further showed that this response was dependent on the presence of a functional internal ear, and that, therefore, this species could be said to hear. But he could not get any response to sound from the smooth dogfish, and so was led to conclude that different fishes might differ widely in this respect, some possessing, some lacking, a true sense of hearing. Since none of the recent investigators who favor the view that fishes hear, have tested the species which, in Kreidl's hands, yielded negative results, it seemed desirable, in the light of recent work, to examine the goldfish again; and this I have undertaken to do. This problem was suggested to me by Professor G. H. Parker, and I am indebted to him for help, suggestions, and criticism throughout the series of experiments.

II. METHODS.

In determining whether or not a fish has a sense of hearing it must be borne in mind that the responses to sound may be very slight and easily confused with responses to other stimuli; and, further, that, although the absence of response does not necessarily mean absence of hearing, the consistent occurrence of a response is fair evidence of the presence of this sense. To test normal goldfishes satisfactorily, it was necessary to isolate them from all other disturbances and to apply the sounding instrument as directly as possible to the water, but without causing any gross mechanical vibration. The apparatus which I used was an aquarium, some 30 cm. wide, 35 cm. long, and 15 cm. deep. The two sides were of glass, and the ends and bottom of clear white pine. The aquarium was placed on a wooden table which stood with its feet on many thicknesses of soft paper, thus isolating it from vibrations which might otherwise reach it through the floor. The bottom of the aquarium was covered on

the inside with a thick layer of cotton wool, which, in turn, was held in place by a sheet of thin cotton cloth to form a deadened floor. On trial, I found that the light entering through the glass sides of the aquarium was a source of disturbance to the fishes. Hence I later made these sides opaque by a covering of dark paper. My method of producing sound was by an electric tuning fork, which was run by a small storage battery and had a pitch of 100 vibrations per second. This was set up on another table, very close to the first one, but not in contact with it. The foot of this table also stood on many thicknesses of soft paper. The fork itself rested on a deadened support, and was so arranged that after it had been set in vibration, it could readily be moved till its base came in contact with the wooden end of the aquarium. This could easily be accomplished without observable jar to the water in the aquarium, and certainly in itself had no effect on the fishes. For when I made the fork, not in vibration, touch the aquarium in the usual way, the fishes gave no reaction, although to the vibrating fork they were very responsive; I tried this many times.

With this apparatus, I tested three classes of goldfishes; (1) normal ones; (2) fishes the greater part of whose integument had been made insensitive by cutting the fifth and seventh nerves, the lateral line nerves, and the spinal cord close to the medulla; and (3) fishes in which the eighth nerves had been cut.

III. Normal Fishes.

Goldfishes appear to be much more irregular in their responses to sound than some other fishes. When one is first placed in the aquarium, it swims about vigorously, darting from side to side in a very restless fashion. This extreme excitability lasts for a considerable time, often an hour; but finally the fish becomes more quiet, sinks to the bottom, and remains nearly motionless except for an almost incessant movement of the pectoral fins. In a few cases, the fishes lay motionless with these fins folded closely to their sides. If now the tuning fork was set in vibration, and brought into contact with the wooden

end of the aquarium, the fishes almost always responded by one of a number of reactions. The most important of these were: a rapid vibration of the tail without locomotion; sudden jerks of the tail from side to side, often so vigorous as to cause a swift dart forward; normal locomotion, forward, backward, or to one side; or in those fishes which lay at rest with the pectoral fins folded, a vigorous spreading of the pectorals. It was evident that individual goldfishes differed from one another in their reactions much more than the individuals of Fundulus as recorded by Parker (:03[a], p. 51). When a fish was tested with the vibrating fork, it might respond by any one of these reactions, but every fish had one distinct reaction characteristic of it, which the application of the fork rarely failed to elicit. Thus, the more active fishes usually responded by vigorous locomotion, the more quiescent ones, by tail or fin movements. Although fishes on which no operation had been performed, usually responded to the sound, one, an albino, and a very sluggish individual, gave no response. The fact that this one died soon after my observations on it were made, is perhaps an explanation of its unusual condition. As an example of the characters of the responses, the following record of ten tests from my laboratory note-book may serve. This record relates to a fish which was subsequently operated upon by cutting the eighth nerves.

1. Tail-jerks, followed by forward swimming.
2. Tail-jerks, then forward swimming after an interval of half a second.
3. Sudden tail- and trunk-jerks, followed by forward swimming.
4. Tail-jerks, but without locomotion.
5. Tail-vibration, but without locomotion.
6. Strong tail-vibration followed by a turn to one side.
7. Tail- and trunk-jerks, followed by forward swimming.
8. Tail-vibration, followed by a sudden turn to one side.
9. Tail- and trunk-jerks, followed by a turn to one side.
10. Tail-jerks, and sudden jump forward.

In all, I made 193 tests on 18 normal fishes, and observed 150 responses, about 78% of the whole. Of the 43 failures, to

respond, 12 were in the case of the albino fish above mentioned, and many of the remaining 31 were probably due to faulty observations caused by the extreme activity of the fishes. In this respect, there is a great difference between different individuals, some being in such continual movement that it is difficult to test them, while others are more generally quiet.

IV. Fishes with Insensitive Skins.

The second class of fishes tested were those in which the greater part of the skin had been rendered insensitive by cutting the spinal cord just posterior to the pectoral fins, as well as both lateral branches of the tenth, and the fifth and seventh nerves on both sides of the body. The fifth and seventh nerves were cut at a point just above the dorsal end of the opercular opening, where they come close to the skin. The fishes were etherized before the operation, and usually recovered and lived many weeks. The individuals selected for this operation were those which showed good pectoral-fin reactions when tested with the tuning fork. Such fishes after recovery lay on their sides on the cloth bottom of the aquarium, and were perfectly quiet unless stimulated. That their skins were practically insensitive was shown by the fact that they were quite indifferent to touch with a bristle or the like.

In 65 tests on 6 such fishes, I observed 52 responses (80%) to the vibrating fork, a condition essentially the same as that of normal fishes. These experiments demonstrate then, that with an almost insensitive skin, a goldfish will respond to sound as a normal fish does.

V. Fishes with Insensitive Ears.

The third class of fishes tested were those in which the eighth nerves had been cut on both sides. In preparing for this operation a number of fishes were tested and only such as showed a clear reaction to sound were operated on. They were etherized, and their eighth nerves were cut by piercing the skull in an appropriate position and cutting downward with a small chisel-

like knife. The chief danger in this operation is in cutting too deep, in which case excessive bleeding may follow. When this was avoided, the fishes usually recovered, and the success of the operation could be judged by their subsequent movements. When they first recovered from the ether they seemed to have lost all power of equilibration, swimming now one side up, and now the other, or resting with their long axes vertical. After about a day, however, they usually acquired and kept their normal position, at least while resting or swimming slowly ; and this ability increases, until after two or three weeks they were, in all their ordinary movements, indistinguishable from normal fishes. If, however, such a fish be placed in a large body of open water and made to swim rapidly, it soon loses all power of orientation and darts about, turning over and over until exhausted. This condition, so far as I know, is permanent, for in the case of one fish which lived for over three months after the operation these reactions showed no tendency to disappear, but persisted till death. The partial recovery of equilibrium noticeable soon after the operation is probably due to a successful attempt on the part of the fish to retain its normal position through sight.

Earless fishes are usually more quiet than normal ones, and hence they can very easily be tested. In all, I made 73 tests on 7 fishes, and in no instance did I get an undoubted response to sound. This is in strong contrast with the reactions of the same fishes before their eighth nerves had been cut, and points beyond question to the ear as an organ of hearing.

I supplemented the foregoing experiments by another series in which two normal fishes that I found to respond well to sound, were etherized, and the eighth nerve of each cut on the right side. After an interval of twenty-four hours, they were both tested again, and found to respond about as well as they did before the operation. In 20 tests on the two, there were 19 responses. They were then etherized again, and the eighth nerves of the left sides were cut. After recovery, they were tested once more, and, although the experiments were conducted with the greatest possible care, not a single response was observed in 20 trials. This experiment shows that the

operation of cutting the eighth nerve, severe as it is, is not sufficiently so to account for even a small part of the reduction in the number of responses which follows the elimination of both ears as sense organs.

In another instance, a fish which before any operation responded vigorously to sound by movements of the pectoral fins, was prepared by cutting two holes in the top of the skull, through which the eighth nerves could conveniently be reached, and the following parts were severed: the spinal cord, the lateral line branches of the tenth nerves, and the superficial portions of the fifth and seventh nerves of both sides. After recovery, the fish gave ten vigorous pectoral fin responses to as many trials with the sounding apparatus. The eighth nerves were then cut, and in twelve tests only one response, and that of a doubtful character, was observed. It, therefore, seems incredible that nervous shock can account for the almost complete loss of response to sound, after cutting the eighth nerves, and I am firmly convinced from the foregoing experiments, that the ear in the goldfish is an organ of hearing, and that it is the loss of this which is accountable for the difference of reaction between fishes in which the ears were intact, and those in which the eighth nerves had been cut.

VI. Discussion of Results.

The results of my experiments differ so essentially from those obtained by Kreidl ('95) that a further discussion of these differences is necessary. So far as reactions to sounds were concerned, Kreidl was unable to distinguish between normal goldfishes and individuals from which the semicircular canals with the attached parts of the ears had been removed. In my experiments, however, while normal fishes responded to sound in about 78% of the trials, those in which the eighth nerves had been cut, scarcely responded at all. The difference between these two sets of results was so great that I determined to repeat, with as much precision of detail as possible, Kreidl's experiments.

I tested several goldfishes, and, having found that they

responded well to the tuning fork, I operated on them in the following way. After etherizing the animals, I cut off the top of the skull, exposing the brain, and the vertical semicircular canals. I then seized the canals with forceps and drew them out bodily with the attached sacs and their otoliths, as Kreidl had done. I operated thus on four fishes, three of which recovered. After recovery, I tested them again with the tuning fork, and found that one responded to the sound about as well as before the operation, and that the two others responded somewhat less regularly than before, though in a still perfectly definite and unmistakable manner. Thus, since these fishes responded like normal individuals, my results confirmed in all essential respects those of Kreidl, and I came to the conclusion that there must be some fundamental difference between Kreidl's methods for the elimination of the ear, and mine. The method I generally used, cutting the eighth nerves, seemed to me a perfectly secure means of excluding the action of the ear. On the other hand, the withdrawal of the semicircular canals with the attached parts of the ear, as practiced by Kreidl, might well leave behind and intact parts of that organ, and thus be inefficient as a method for completely excluding the ear. To settle this matter, I made careful dissections of the ears of goldfishes. The ear of the goldfish is in all essential respects similar to that of Cyprinus, as described and figured by Retzius ('81, p. 78). The semicircular canals are of large size; the two vertical canals lie free in the brain cavity, while the horizontal canal is partially imbedded in the skull. The sac into which these canals open, the utriculus, is of medium size, and contains a large lenticular otolith. The utriculus, with its otolith lies free in the brain cavity and is the structure which is removed in connection with the semicircular canals in fishes which are operated on by Kreidl's method. But ventral to these parts, and largely imbedded in bone is another portion of the internal ear, which probably represents the combined sacculus and lagena. This is not removed, nor even seriously disturbed by the Kreidl operation. This deeper sac extends posteriorly and ventrally until that of the right ear nearly meets that of the left in the base of the cranium. Each sac contains two otoliths, one long and

rod like, lying for the most part in the saccular portion, the other lenticular in outline, and lodged in the lagena proper. The wall of this sac is supplied with branches from the eighth nerve and is so surrounded by bone that all attempts to remove it by pulling out the semicircular canals were complete failures. In the four fishes on which I operated by Kreidl's method, subsequent dissection showed these structures intact. Thus, his operation leaves uninjured a large part of the internal ear, in fact, just that part which, from comparison with the ears of higher vertebrates, would be expected to be concerned with hearing. I believe, therefore, that Kreidl's method of operating is defective, and the reason that the fishes upon which he had operated responded to sounds much as normal ones did, was not because in both cases the skin was stimulated, as he believed, but because his so-called "earless" fishes still retained intact a part of the ear which, as I have already shown, acts as an organ of hearing. That it is such an organ follows from the fact that when its nerve connections are cut, the responses to sound cease.

VII. Summary.

1. Normal goldfishes usually respond in a definite manner to sound-vibrations in water.
2. Goldfishes in which most of the skin has been rendered insensitive by cutting the nerves, and specimens from which the ears, except the saccular portion, have been removed still respond in an essentially normal way to sound vibrations in water.
3. Goldfishes in which the eighth nerves have been cut on both sides, thus eliminating the sacculi and lagenæ as well as the rest of the ear, seldom or never respond to sound vibrations in water.
4. Goldfishes possess the sense of hearing, and the portion of the ear concerned with this sense is the sac which probably represents the sacculus and the lagena of higher vertebrates.

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